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The development and behavior of the chromosomes in the first or heterotypic mitosis of the pollen mother-cells of Allium cernuum Roth

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(WITH PLATES 23 AND 24)

It may seem to the reader of cytological literature that whoever offers a contribution upon *Allium* might well preface his remarks with an apology for so doing. However, certain favorable forms of both plants and animals will doubtless ever remain objects of investigation. On looking about for favorable material for class use, the senior author came upon a species of wild onion, common in certain localities in Indiana, namely, *Allium cernuum* Roth, a species which is regarded as more favorable than the much used *Allium Cepa*.

A study of mitotic phenomena has been made in both vegetative and microspore mother-cells, and the results obtained and conclusions reached differ so much in certain respects from those of Bonnevie ('11), as set forth in a recent contribution on *Allium Cepa*, that we have decided to present the results of our observations on the pollen mother-cells at this time, reserving an account of the process of nuclear behavior in vegetative cells for a future publication.

In describing the resting stage of the nucleus in the pollen mother-cell of *Allium Cepa*, Bonnevie ('11, 197) asserts that a number of threads radiate from a chromatin knot or lump (Chromatinknoten), being continued into the meshes of the nuclear net. "Vom Chromatinknoten sieht man eine Anzahl Fädchen, die in den Maschen des Kernnetzes ihre Fortsetzung finden, radiär ausstrahlen." With the disappearance of the anastomoses between these radiating threads, the latter gradually became more distinct throughout their entire length, at the same time appearing always zigzag or spirally twisted. Precisely the same structure is reported for the resting nucleus of somatic cells. Following this structure there takes place (l. c. 197) a pairwise conjugation of the chromosomes, which finds its culmination in synapsis. This conjugation is accomplished by the lateral fusion in pairs of the threads radiating from the chromatin knots (l. c. fig. 20). Soon after this (l. c. 198) such nuclei become more irregular, for, in addition to the chromatin knots or lumps, there appear other dense accumulations of chromatin, so that, as a result, the original radial arrangement of the threads is no longer recognizable (l. c. fig. 21).

In the light of their own preparations as compared with Bonnevie's figs. 18–21, the writers are convinced that Bonnevie is describing the appearance of very poorly fixed and poorly stained nuclei. That Bonnevie has failed to distinguish between good and bad fixation is clear to the writers from the following (l. c. 198): "Ja, das Zusammenlaufen der Chromatinsubstanz kann soweit gehen, dass alles Chromatin des Kernes in einer einzigen, optisch schwer analysierbaren Masse zusammengeballt erscheint." This is true, but such phenomena do not represent normal steps in the mitotic process; they are largely artifacts. It is true, as has been pointed out some years ago by one of us (Mottier, '07, fig. 15), that chromatin granules may sometimes form accumulations either by themselves or grouped about the nucleolus, but such phenomena are to be regarded more on the order of chance occurrences than as representing significant and regularly appearing stages of the nucleus. It is conceivable that such accumulations of chromatin granules may be run together or fused by the reagents, and it is highly probable that the Chromatinknoten were formed in this manner. We do not find these masses of chromatin in our preparations. At any rate the Chromatinknoten of Bonnevie's figs. 18–21 are not to be regarded as of any consequence in the normal process of mitosis, as will be seen from what follows.

THE RESTING NUCLEUS AND SYNAPSIS

The nucleus of the resting stage in the pollen mother-cells of *Allium cernuum* Roth presents the well-known net or reticulum of linin upon which are distributed with more or less regularity the chromatin particles or granules. From one to several nucleoli of varying sizes are present. FIG. 1 illustrates the structure of the nucleus in a pollen mother-cell soon after the last somatic division. The structure of the whole cell is the same as that of any somatic cell from any meristematic region. The growth period of both cell and nucleus now begins, and the very marked increase in the size of the nucleus as compared with that of the cell is very conspicuous in this as well as in other species of *Allium* (FIG. 2, 7, 8, 9). In FIG. 2 the nucleus is almost if not quite as large as it ever becomes. The nuclear reticulum is uniform, and the nucleoli may or may not be evenly spaced in the cavity of the nucleus. They do not lie in the same plane, and in making the drawing the focus was necessarily changed. FIG. 2 and all others represent rather thick sections of cells. Sometimes the chromatin granules form larger and smaller aggregates, which may be grouped about the nucleoli or removed from the latter, but we do not find large fused masses of chromatin such as Bonnevie has figured and described as "Chromatinknoten." A glance at FIG. 2 shows further that there may be a tendency to form a thread, that is, there will be seen stretches of linin in which the granules are arranged in lineal series. As pointed out by one of us (Mottier, '07) for *Lilium Martagon*, there is a tendency in *Allium cernuum* to form a delicate thread or spirem just before or as the nucleus passes into the synaptic contraction. FIG. 2 is about ready to begin the contraction of its net into the compact mass. FIG. 3 is a faithful attempt to illustrate the nuclear structure passing into synapsis, and FIG. 4 is a similar stage but includes the whole nucleus. These two figures were found in the same section of the loculus, in which were to be seen variously different stages of the early contraction. The writers wish to state most emphatically that there is no evidence of the fusion of two spirems during the contracting process. The spirem is formed directly from the nuclear network in the only way possible for a net to make a continuous thread, namely, by the breaking or dissolving of threads of certain meshes and the fusion of others. In the fusion of meshes several threads are seen to unite just as frequently and as certainly as one may find the fusion of only two threads. The appearance of the lateral union of two threads of certain meshes in several parts of the nucleus previous to synapsis is the strongest evidence, in the opinion of the writers, that those observers can bring forward who hold to the doctrine that two spirems fuse side by side during, or prior to, synapsis and who deny that the somatic chromosomes are arranged end to end in a lineal series to make the continuous hollow spirem. These authors ignore the fact that three or more threads fuse in the formation of the spirem from the net as well as only two, and as will be pointed out in a subsequent paragraph, they omit from consideration and from their series of figures the most difficult and perhaps the most important steps in the formation of the bivalents from the hollow spirem.

FROM SYNAPSIS TO THE BIVALENTS

The stage of FIG. 4 passes directly into the closely contracted mass of FIG. 5. While the chromatin is still in this state, the thread gradually shortens and thickens into a heavy cord. Even before an appreciable loosening up of the synaptic ball it is readily seen that a thick spirem, or cord, is forming from the slender thread, and, as soon as the contracted mass loosens (FIG. 6), the correctness of this interpretation is beyond doubt. We have in our preparation transitional stages between FIG. 5 and 6, but it was not deemed necessary to include these in the series. The thick cord thus developed now becomes distributed throughout the nuclear cavity. In *Allium* it is relatively thick, apparently rather uniform in structure, though sometimes lumpy, and in many cases numerous delicate threads extend from the spirem to the nuclear membrane or between adjacent or parallel portions of the cord (FIG. 7, 8). A nucleolus is usually present. At this stage a longitudinal split may be sometimes seen, but this phenomenon is rather the exception than the rule (FIG. 8). This fission always closes up and the two halves become so closely applied or fused that the double nature of the thread, if really present, is completely concealed before any indication of cross segmentation is discernible.

Following the stage of the loose hollow spirem, the same undergoes a rearrangement before transverse segmentation, which results in a twisting, looping, and an entangling of its parts. This phenomenon found in the lilies and in other plants is known as the second contraction. In the lilies there is a central knotted or entangled portion of the spirem from which extend somewhat radially loops and straight stretches of the cord, the latter with free ends. In *Allium cernuum* we do not find this typical appearance observed in *Lilium*. There is usually a tendency for the spirem to mass or become more closely entangled near the center of the nuclear cavity with a looping in the freer parts as shown in FIG. 10 and 11, which represent the less complicated condition, but, as a rule, the entanglement is so complicated that it is not possible to follow definitely more than a few loops or turns of the entire cord. If, for example, the spirem of FIG. 10 or 11 were bunched together more closely near the center with a greater twisting of the loops, we should have the more complicated state referred to above. The complexity of this step is increased by the fact that the spirem usually becomes more lumpy, or thicker places alternate with others more attenuated, just prior to, or as this rearrangement is ushered in (FIG. 9). Sometimes when the rearranged condition is not too confused, the spirem seems to be undergoing cross segmentation (FIG. 10), but whether this is the rule we are unable to say. It is certain, however, that in all, or in nearly all cases, the transverse segmentation of the spirem is accomplished during the entangled condition, or the stage of the second contraction. As segmentation is taking place there is always a violent twisting about each other of the two members of the bivalents, for as soon as the bivalents can be recognized as such, they invariably present the appearance of FIG. 12, save that they are more closely bunched together. Ordinarily they are heaped up in a more compact mass. For the illustration we have selected a nucleus in which a less entangled massing of the bivalents is present (FIG. 12).

That each bivalent, or the majority of them, represents a loop of the spirem, the two sides of which have twisted about each other, and not the two halves of the longitudinally split spirem, is in our opinion beyond question. The longitudinal split of the thread seen in the spirem disappears from sight, and, if it be present during the stages described, the two halves are so closely applied that no trace of the fission can be seen. Almost without exception the two members of each bivalent are twisted about each other, some tightly, others loosely (FIG. 12, 13). In all cases the bivalents, as soon as formed, are massed and entangled into a confused heap.

Later they separate and become irregularly distributed within the nuclear cavity (FIG. 14). At the same time they show a tendency to untwist, and as this is brought about the fact that many represent loops of the spirem is strikingly manifested.

Bonnevie figures the looped and twisted condition of the bivalents, but the manner in which they originate from the spirem is not satisfactorily shown. In fact Bonnevie does not seem to have taken cognizance of the stages which we have described as the rearrangement of the spirem, or the second contraction, and this author has not, in our opinion, shown how her FIG. 33 is derived from FIG. 30. In our opinion her figures not only disprove the very thing she attempts to demonstrate, but lend support to the view set forth in the foregoing paragraphs, namely, that the two members of each bivalent represent pieces of the spirem that were previously arranged end to end and not the longitudinal halves of parts of the spirem.

At the time of cross segmentation of the spirem the chromosomes have attained their largest size.* During the formation of the spindle and later they seem to undergo a condensation by which their size is much reduced. Their number is seven or eight. While seven only were counted in some cases, the writers are inclined to regard eight as the correct haploid number.

FROM SPINDLE TO DAUGHTER NUCLEI

As is so well known, the spindle develops first as a multipolar complex which gradually becomes bipolar. Within the complex of spindle fibers the chromosomes are usually crowded so that the transition from the tightly twisted state of the two members to the large open ring-shaped structure that appears rather constantly in the equatorial plate of the mature spindle, is not readily followed (FIG. 15–17). The ring-shape of the bivalents in the spindle is doubtless the most striking phenomenon in the whole mitotic process of *Allium cernuum*. This form of chromosome is brought about by the fact that the chromosomes are attached to the spindle fibers at a point about midway between the ends. As the two members of each bivalent thus attached are drawn apart by the spindle fibers, each is bent at the place of attachment and a ring results. In FIG. 16 some of the rings are seen from the edge while others have their flat sides turned toward the observer. In many of these rings it is still very evident that they were loops of the spirem as shown above. However, the open or closed ring is not the only form seen in the spindle stage. Sometimes the bivalents appear as two straight or crooked rods attached at or near the ends to the fibers, or **X**- and **Y**-shaped forms may appear.

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* The reader should bear in mind that FIG. 9, 10, 11, 12, 14, 18 and 19 are more highly magnified than FIG. 13, 15, 16, 17, etc.

One of the most conspicuous phenomena in the whole mitotic process of this species, and one which is very significant when viewed in the light of the kinetic processes involved in mitosis, is the shape of the chromosomes just before the appearance of the multipolar spindle and at the stage of the mature spindle (Fig. 13, 16, 17). In FIG. 13 the members of each bivalent, or at least the large majority of them, are tightly twisted about each other, while in FIG. 16 and 17 they appear just as uniformly as open rings. The question arises: what kinetic forces are responsible for the twisting in FIG. 13, and what for the condition of FIG. 17? A discussion of this interesting question would extend far beyond the limits of this paper, and we shall merely venture the opinion that neither magnetic nor osmotic activities seem applicable to the phenomena under consideration.

During metakinesis, that is, just at the instant when the segments are separated, each shows its longitudinal fission. Each half-ring, which is made into a **U** by the pull of the spindle fibers, is now a double **U**. Frequently just before metakinesis this longitudinal fission can be seen when the free ends of the bivalent are turned directly toward the observer (FIG. 18). In FIG. 19, an anaphase, the double **U**-like nature of the daughter segments is clearly shown. It may be remarked in passing that the large size and elongated form of the chromosomes of the mature spindle, and the fact that the halves of the **U**'s and **V**'s tend to separate from each other during the anaphase, make counting perplexing and uncertain, in spite of the large size and small number.

The shape and position of the various chromosomes as they pass to the poles seem to speak strongly in favor of a pull being exerted by the spindle fibers, which are in reality fine colloidal threads and not expressions of osmotic currents. In fact it seems extremely difficult to bring any of these phenomena under explanations based upon osmotic activity.

On arriving at the poles, the chromosomes become closely crowded together in a manner well known for nearly all plants. In the organization of the daughter nuclei, the chromatin does not pass into the finely divided state by the processes of reticulation, alveolization or fragmentation as is characteristic of many gymnosperms and dicots. The various segments do elongate, however, to three or more times their original dimensions, becoming somewhat lumpy or irregular in outline, and finally form a sort of interrupted spirem which is seen as a series of longer or shorter loops or turns passing from the pole to the anti-pole side of the nucleus (FIG. 22). This figure represents a daughter nucleus seen somewhat obliquely from the polar side. The course of the spirem is usually more irregular than in this figure, there being many more short and abrupt genuflections or kinks. We have spoken of this spirem as discontinuous, for the reason that what are regarded as free ends can be found. These free ends are sometimes joined by very delicate threads like the anastomosing threads extending between parallel parts of the spirem in all cells whether purely vegetative or sporogenous. If the apparently free ends were connected by thicker threads, the spirem could then be spoken of as continuous. Whether or not this spirem is continuous or interrupted is of no theoretical importance. The side of each loop, or turn, is wavy or zigzag, due, of course, to the lack of space in the nuclear cavity for the placing of the greatly elongated segments. Whether continuous or interrupted, the whole forms a sort of crown or wreath open both at the pole and anti-pole sides. We assume that the adjacent or parallel sides of the loops are homologous with the sides of the **U**'s or **V**'s that pass to the poles during the previous anaphase. We do not find that the loops or ends of this spirem unite at the polar side to form "Chromatinknoten" either in these nuclei or in somatic cells that are normally preserved. A comparison of a daughter nucleus (FIG. 22) with a granddaughter nucleus (FIG. 23) shows that the arrangement of the chromatin is similar and that it is due to similar causes which may be and probably are purely mechanical.

SUMMARY

The resting nucleus prior to synapsis consists of a reticulum of linin and chromatin granules and of one or more nucleoli. The "Chromatinknoten" of Bonnevie are not present.

Before synapsis there is, as in *Lilium*, a tendency to form a delicate continuous thread or spirem. There is no union of two spirems in synapsis.

Synapsis is a real contraction of the nuclear net and not a growing away of the nuclear membrane from the nuclear network as claimed by Lawson.

The spirem is a direct transformation from the nuclear net.

The hollow spirem is a thick chromatin cord in which a longitudinal split is only occasionally seen and only in parts of the same. This split whenever present always closes up completely before the cross segmentation.

The rearrangement of the spirem takes place which is referable to the *second contraction* described for the lilies and other plants. This results in an entanglement of loops and parallel parts of the spirem which twist upon each other. During this rearrangement the transverse segmentation of the spirem occurs.

Each bivalent chromosome is formed by an approximation, usually side by side, of different lengths of the spirem, which may have appeared as loops or otherwise. Each bivalent is, therefore, to be regarded as two somatic chromosomes that were *previously arranged end to end in the spirem.* The approximation of two somatic chromosomes, side by side, or otherwise, or their adherence end to end to form bivalents, is not known as *synapsis* in botanical literature, nor is it properly called a conjugation.

The prevalent form of bivalent upon the mature spindle is the large ring, although other forms exist.

The daughter segments split longitudinally during metaphase. This fission may be looked upon as a preparation for the second, or homotypic, mitosis.

In the construction of the daughter nuclei, the chromatin does not pass into a finely divided state. The chromatin segments elongate greatly, becoming wavy or zigzag, and form an interrupted spirem by the union of a number of the free ends. This spirem is disposed in the form of a wreath or crown open at both the polar and antipolar sides. The ends of the chromatin segments do not fuse into "Chromatinknoten" in the daughter nucleus.

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Explanation of plates 23 and 24

All figures were drawn from sections with the aid of the Abbé camera lucida and with Leitz 1/12 immersion and ocular IV or with Zeiss apochromatic immersion 2 mm., apert. 140, and compensating ocular 12. Magnification of figures 3, 4, 9, 10, 11, 12, 14, 18 and 19 about ×2000; all other figures about ×1600.

FIG. 1. Young pollen mother-cell soon after the last somatic division.

FIG. 2. Pollen mother-cell near the close of the period of growth. The nucleus is almost as large as it ever becomes.

FIG. 3. A thin section of a nucleus passing into synapsis; the net-work is forming a thread or spirem.

FIG. 4. A similar stage, showing nearly the whole nucleus. These two figures were near each other in the same section.

FIG. 5. Synapsis is complete.

FIG. 6. The synaptic mass loosening up. The very long, slender thread has shortened into a thick cord.

FIG. 7. The thick, hollow spirem.

FIG. 8. The same stage as FIG. 7. A longitudinal split is seen in two or three places.

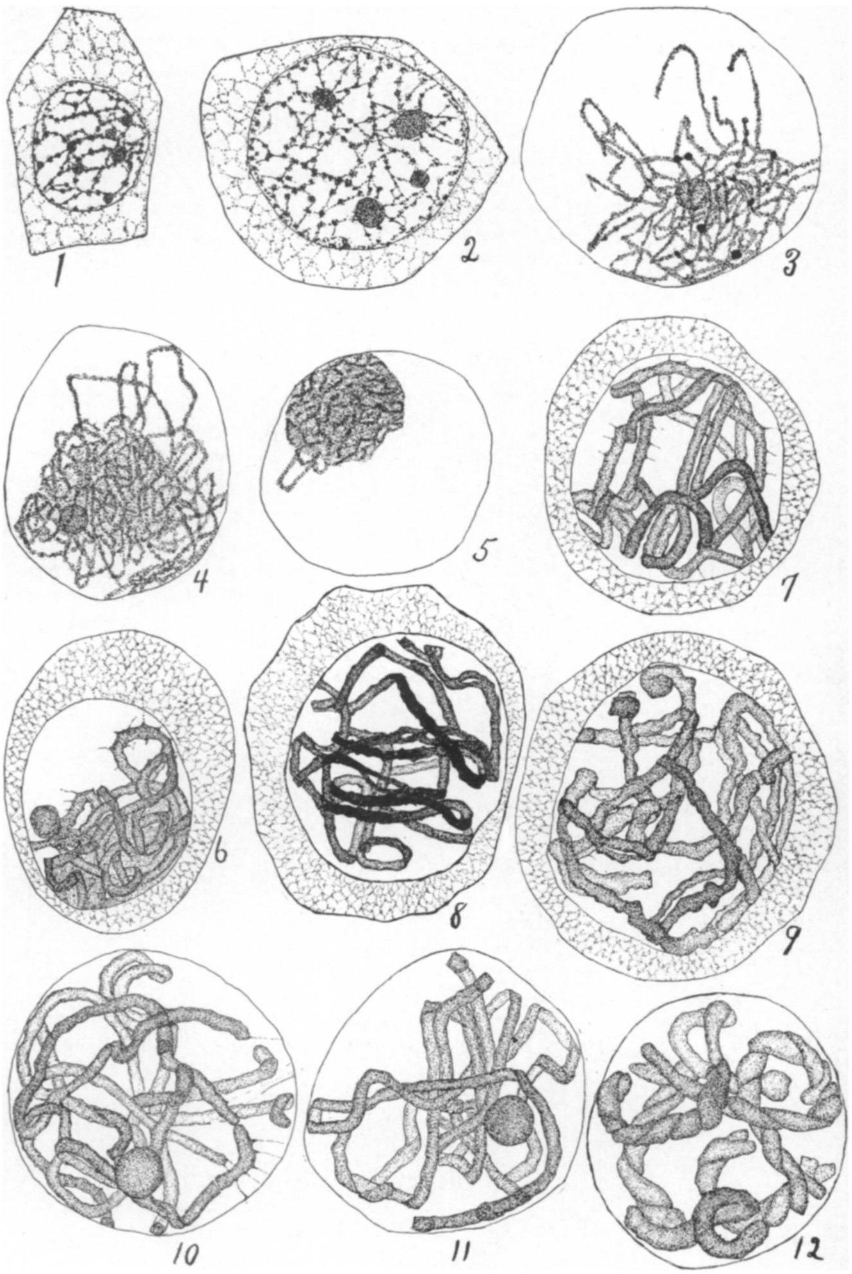
FIG. 9. The spirem as it frequently appears before the rearrangement into the second contraction. At this stage the spirem may appear lumpy or with thicker and thinner portions.

FIG. 10, 11. Initial steps of the rearrangement. The chromatin cord is, as a rule, much more entangled than in these figures. Indications of transverse segmentation are seen in FIG. 10.

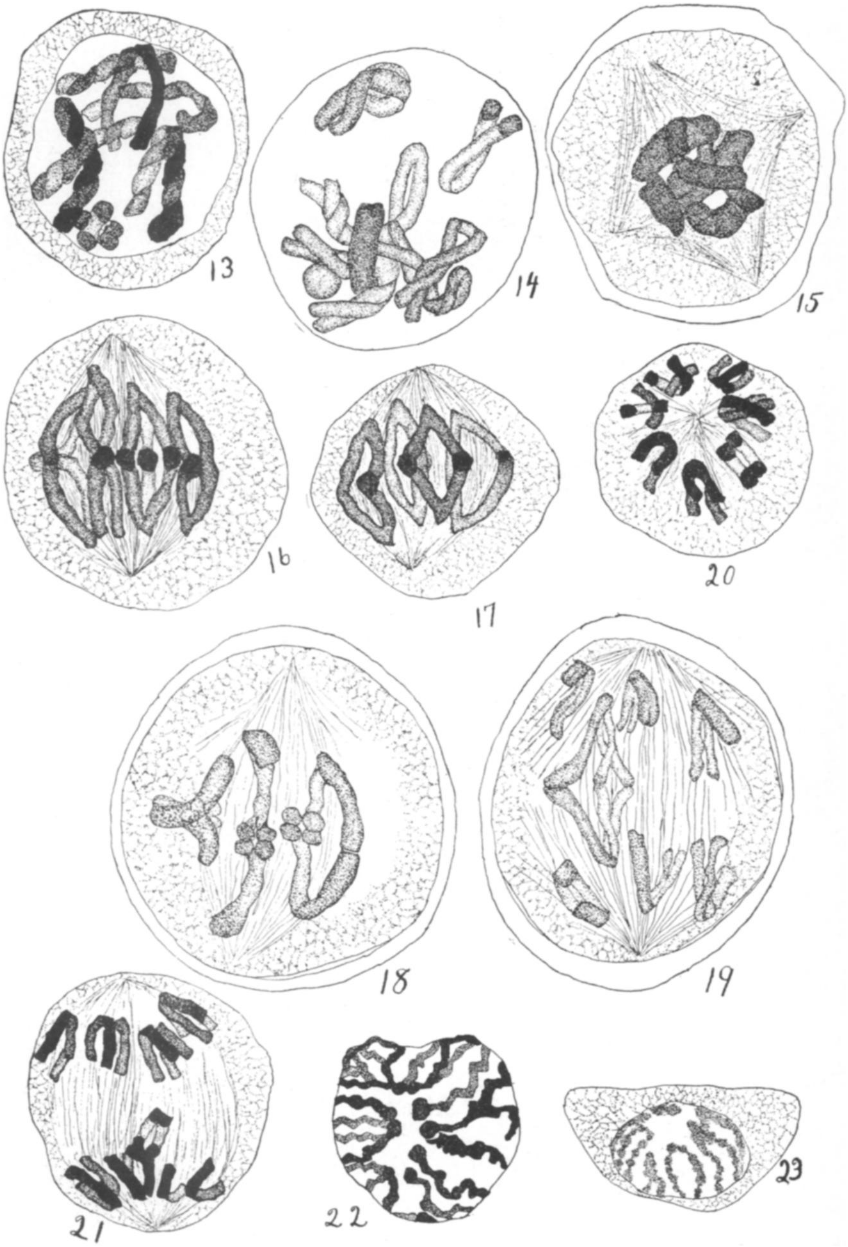
FIG. 12. Segmentation is about completed. The two members of each bivalent are twisted about each other.

FIG. 13. Similar to the preceding; the twisting is more pronounced in all chromosomes.

FIG. 14. Chromosomes beginning to untwist preparatory to the formation of the spindle.



MOTTIER AND NOTHNAGEL: CHROMOSOMES OF ALLIUM CERNUUM



MOTTIER AND NOTHNAGEL: CHROMOSOMES OF ALLIUM CERNUUM

FIG. 15. Multipolar stage of spindle.

FIG. 16, 17. The fully developed spindle. Nearly all of the chromosomes are rings.

FIG. 18. Spindle showing three chromosomes with the metaphase beginning. At the right a ring-shaped chromosome seen flatwise. In the center the two somewhat curved members of the bivalent are stretched out tangentially upon the spindle. The four free ends seen in these two chromosomes are indications of the longitudinal split. The chromosome at the left is a ring seen from the edge.

FIG. 19. An anaphase; the longitudinal fission of each daughter chromosome is very evident.

FIG. 20. A polar view of an anaphase. The halves of the longitudinally split daughter segments tend to separate.

FIG. 21. A typical anaphase in longitudinal section.

FIG. 22. A polar view of a daughter nucleus showing arrangement of the spirem into a system of loops.

FIG. 23. One cell of a tetrad, or granddaughter cell. The disposition of the chromatin is the same as in the daughter cells at the corresponding stage.